PALEONTOLOGIA

PRIMATE FAUNA FROM THE MIOCENE LA VENTA, IN THE TATACOA DESERT, DEPARTMENT OF HUILA, COLOMBIA

by

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RESUMEN

Los ejemplares aquí descritos aumentan el conocimiento sobre la diversidad de los primates del Mioceno medio de América del Sur. Nótese, sin embargo que se discutirá y se mencionará sólo el material que ya ha sido descrito previamente; el resto de fósiles se prepara para otra publicación (Setogouchi y Rosenberger, en preparación), razón por la cual no se mencionan en este manuscrito. Estos datos proporcionan un panorama más claro sobre la diversificación de la fauna primatológica durante el Mioceno medio.

En esta área, ahora periférica a la Cuenca del Amazonas, donde los primates platirrinos son muy abundantes, pudieron haber vivido 10 especies, en forma simpátrica, sin tenerse en cuenta las diferencias temporales. El arreglo adaptativo de insectívoros-frugívoros-folívoros que tipifica las comunidades del bosque Neotropical en la actualidad, parece guardar similitud con las comunidades de primates fósiles de La Venta. Estos fósiles también pa-

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recen corroborar la hipótesis (ROSENBERGER, 1979; DELSON & ROSENBERGER, 1984) de que los géneros de monos vivientes del Nuevo Mundo *(Callithrix, Alouatta y Ateles)* representan una rama filogenética que se separó hace mucho tiempo y que guarda una estrecha relación con los fósiles encontrados en el sitio Kyoto en La Venta, los cuales, posiblemente fueron sus ancentros.

1. INTRODUCTION

The Tatacoa desert in Department of Huila of Republic of Colombia, is one of the richest classical continental South American localities yielding Tertiary vertebrate faunas, known as the La Venta fauna. The La Venta is within the Miocene Honda Group and its fauna has been correlated with Argentine deposits of the Friasian Land Mammal Age, dated at about 14 Ma (million years ago). The original collection yielded three primate species: *Neosaimiri fieldsi, Cebupithecia sarmientoi,* and *Stirtonia tatacoensis.* Other fossil platyrrhine primates are known by four or five additional genera from the early Oligocene through early Miocene of Bolivia and Argentina, and small collection of Caribbean subfossils.

Beginning in 1976, further exploration of this area was undertaken by a joint expedition of the Primate Research Institute of Kyoto University (Japan) and Ingeominas. With the collaboration of scientists at the Universidad Nacional de Colombia and the University of Illinois at Chicago, USA. The express intention of this project is the recovery of more Tertiary platyrrhines. Included among the many vertebrates discovered during the past six fields seasons are representatives of primate taxa that were already known and several new genera and species. Now, the La Venta primate assemblage may amount to nearly ten genera.

The La Venta fossils appear to support the hypothesis that the living New World monkey genera represent separate long-lived lineage, for Callitrichinae, *Saimiri, Pithecia-Cacajao, Alouatta, Ateles* and *Brachyteles* each appear to have their closests relatives, and possibly their ancestors, represented in this fauna. Most recently, the first fossil remains of a marmoset, *Micodon,* have been recovered, providing direct evidence bearing on phylogeny and the evolution of size and occlusion in the Subfamily Callitrichinae.

2. AGE OF THE FAUNA

The geology of the area, known as the La Venta, has been studied by Fields (1959) and, more recently, by Takemura (1983) and Hayashida (1984). The notes on geology has already been published elsewhere (Setoguchi & Rosenberger, 1985a).

All the specimens treated here have been discovered in the single spot, now called the Kyoto Site, within the Monkey unit of the Honda Formation, in the La Venta badlands. The Kyoto Site was discovered in the field season of 1982. The fossils were recovered from a siltstone lens, 1 m in diameter and about 50 cm thick.

Samples for paleomagnetic measurements were collected from 14 sites at La Venta and from 5 sites at El Dinde (Hayashida, 1984). Most of the sites show normal magnetic polarity. Reversed polarity was found only in two sites, one at the uppermost horizont of the Honda Group and the other within the overlying Gigante Formation. The normally magnetized sites compose a thick normal magnetozone covering the middle to upper part of the Honda Group. The long normal magnetozone of the Honda Group may be assigned either to Epoch 9 (from 8.8 to 10.3 Ma) or to Epoch 15 (from 13.6 to 15.2 Ma) (Lowrie & Alvarez, 1981).

Biostratigraphically, the La Venta fauna is assigned to the Friasian Land Mammal Age of South America (Hirschfeld & Marshall, 1976). Marshall *et al.,* (1977) obtained K-Ar ages ranging from 14.0 to 15.4 Ma from volcanic rocks in the Collon Cura Formation in which Friasian stage is defined by a few local faunas. Recently, three volcanic tuffs in the normal magnetozone of the Honda Group are dated 16.1 ± 0.9, 14.6 ± 1.1 and 15.7 ± 1.1 Ma, respectively by zircon fission-track age determination (Takemura & Danhara, 1985).

These results confirm the biostratigraphical correlation of the La Venta fauna to the Friasian fauna, dated at about 14 Ma. And also they confirm the paleomagnetic correlation of the normal polarity interval in the Honda Group to a part of Epoch 15, 15.2 to 13.6 Ma, not to Epoch 9.

3. TERMINOLOGY

Occlusal terminology follows the system of van Valen (1966), with such modifications as can be found in Szalay (1969), Szalay and Delson (1979) and Rosenberger and Kinzey (1976). Our taxonomic nomenclature for family-level groups differs from that which is generally found in the literature dealing with ceboid primates, for it is based upon a revised classification of the group (Szalay and Delson, 1979; Rosenberger, 1981). It can be summarized briefly with geochronological positions of fossils indicated: Cebidae: Cebinae=*Cebus, Saimiri, "Saimiri" bernensis* (Pleistocene), *Neosaimiri* (M. Miocene), *Dolicchocebus* (L. Oligocene); Callitrichinae = *Callithrix, Cebuella, Leontopithecus, Saguinus, Callimico, Micodon* (M. Miocene). Atelidae: Atelinae=*Ateles, Brachyteles, Lagothrix, Alouatta, Stir-*

tonia (M. Miocene), *Kondous* (M. Miocene); Pitheciinae = *Pithecia, Chiropotes, Cacajao, Callicebus, Aotus, Cebupithecia* (M. Miocene), *Xenothrix* Pleistocene, *Homunculus* (E. Miocene), *Tremacebus* (L. Oligocene). The early Oligocene *Branisella* is placed Family incertae sedis.

All the specimens treated here are housed in INGEOMINAS. The abreviation, IGM-KU, refers to INGEOMINAS and the Kyoto University Primate Research Institute.

4. PRIMATE FAUNA OF THE LA VENTA

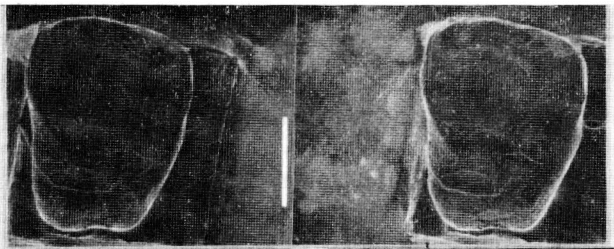
Some of the primate fossils recovered by the joint expeditions of Kyoto University and INGEOMINAS have already been described (Setoguchi, 1985; Setoguchi & Rosenberger, 1985; Setoguchi, 1986). Some of them were translated into Spanish (Setoguchi *et al.*, 1983; Setoguchi & Cadena, 1984; Setoguchi *et al.*, 1985). The rest of the fossils are now being prepared for publication elsewhere (Setoguchi & Rosenberger, in preparation). The only materials which have already been described elsewhere are mentioned and discussed in this paper.

Order Primates Linnaeus, 1758
Superfamily Ceboidea Bonaparte, 1831
Family Cebidae Bonaparte, 1831
Subfamily Callitrichinae Thomas, 1903
Genus *Micodon* Setoguchi & Rosenberger, 1985
Micodon kiotensis Setoguchi & Rosenberger, 1985
(Figs. 1 & 7)

Material: IGM-KU-8401, left M^1 (type).

Remarks: *Micodon* is the smallest primate heretofore found in the La Venta fauna, and within size range of *Saguinus* and *Callithrix*. It differs from most callitrichines in the generally low-relief morphological pattern, large size of the talon basin, and particularly, the considerably large size of hypocone. The morphology and position of the hypocone is distinctly different from the conditions found in such genera as *Callimico* and *Saimiri*. By comparison with *Micodon*, the hypocone is far smaller in *Callimico*, where it appears as an excresence of the lingual cingulum. This cusp is more developed in *Saimiri*. Overall, the *Micodon* M^1 shows some gross resemblances to certain *Saguinus*, although none of the specimens we have examined hardly approach this fossil in hypocone development.

Micodon is clearly within the size range of living marmosets but is well below the size range of larger marmosets, such as *Callimico goeldii* and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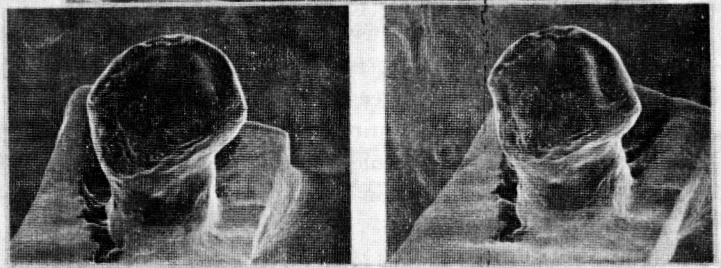
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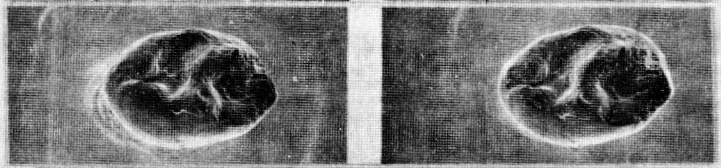
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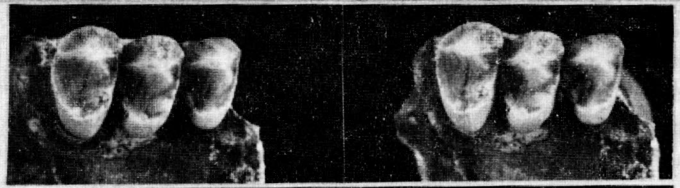
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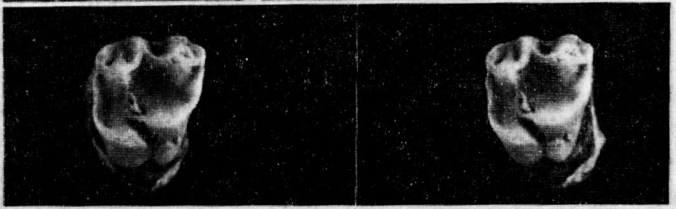
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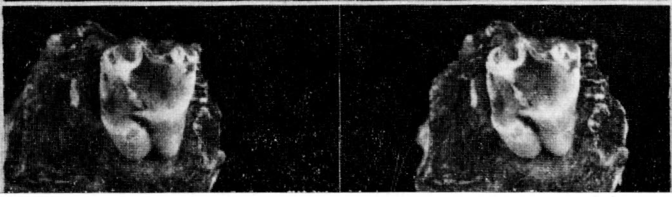
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FIGURA 1. *Micodon kiotensis,* IGM-KU-8401, left M^1 (type). Occlusal view (stereo pair).

FIGURA 2. Genus indet., IGM-KU-8402, right I^1. Lingual view (stereo pair).

FIGURA 3. Genus indet., IGM-KU-8403, left P_4. Occlusal view (stereo pair).

FIGURA 4. *Stirtonia tatacoensis,* IGM-KU-III-1, from right to left, right P^2, P^3 and P^4. Occlusal view (stereo pair).

FIGURA 5. *Stirtonia tatacoensis,* IGM-KU-III-1, right M^1. Occlusal view (stereo pair).

FIGURA 6. *Stirtonia tatacoensis,* IGM-KU-III-1, right M^2. Occlusal view (stereo pair).

Leontopithecus chrysopygus. Since the callitrichines are probably a modified radiation that underwent their major diversification at a small body size, we consider it very likely that *Micodon* is a marmoset. The *Micodon* M^1 suggests that body size/tooth size reduction preceded the loss of the hypocone cusp. It has been argued that the combination of tricuspid molars and small size literally define a marmoset phyletically (Hershkovitz, 1977). On the other hand, *Callimico* is a four-cusped ceboid whose anatomy suggests that it is cladistically closest to the tricuspid marmosets, and alternative schemes of platyrrhine phylogeny place the four-cusped cebines, *Cebus* and *Saimiri,* as the sister-taxon of the entire group. The upshot of these latter views is that a four-cusped molar would be fully expectable in small, ancestral callitrichine, and even in callitrichin sister-group.

Genus indet.

(Figs. 2 & 8)

Material: IGM-KU-8402, right I^1

Remarks: The size of the tooth is close to or within the expected ranges of variation of forms like *Callimico goeldii, Callithrix jacchus* and *C. aurita*. In lingual view, a prominent torus is developed at the center of the fossa. It becomes broader and thicker towards the base of the tooth. The torus is separated from the thickened enamel along the apical margin of the crown, leaving valleys or foveae mesially and distally on both its sides. Thus, this incisor is characterized by a bifoveate lingual surface.

In most living ceboids, the shape of the I^1 lingual surface is essentially planar or biconcave. The lingual surface serves as an enlarged expanse into which the contiguous apical margins of I_1 and I_2 occlude in tandem. Thus the four mandibular incisors articulate together as a single arched unit into right and left I^1s. In *Callithrix* and *Cebuella,* however, there is a mesiobasal thickening of the crown and the I^1 lingual fossa is divided into two separate fovea by a midcentral prominence. This is unique situation, resembling only some *Leontopithecus* in an abstract way. The lower incisors of *Callithrix,* therefore, do not articulate with a continuous I^1 depression, that is, I_1 and I_2 occlude independently into the mesial and distal foveae, respectively.

The glove-like morphology of the La Venta incisor bears considerable resemblance to the derived morphology of *Callithrix* and *Cebuella*. All share in common the development of a lingual torus, dividing the lingual surface into two occlusal depressions and so on. Consequently, we consider the fossil to belong either to the *Callithrix/Cebuella* clade or, less likely, the

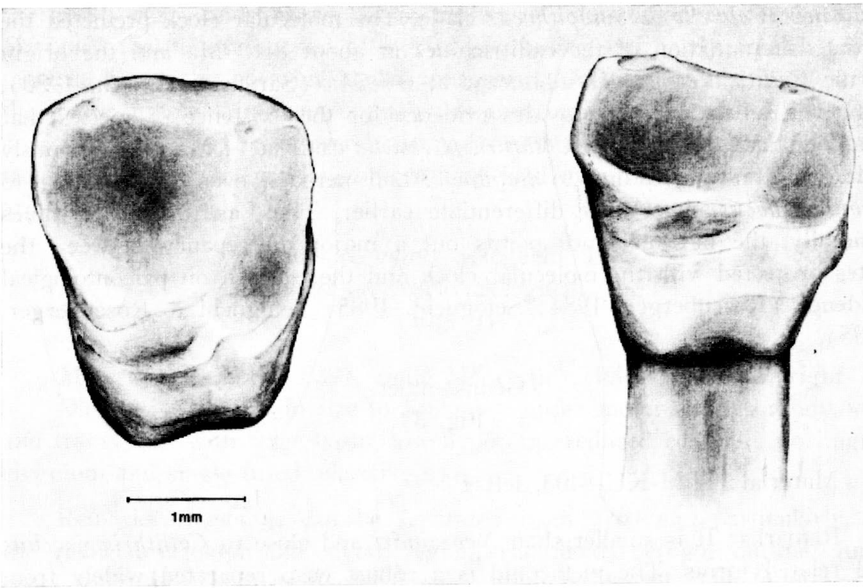

FIGURA 7. *Micodon kiotensis,* IGM-KU-8401, left M^1 (type). Left: Occlusal view; Right: Lingual view.

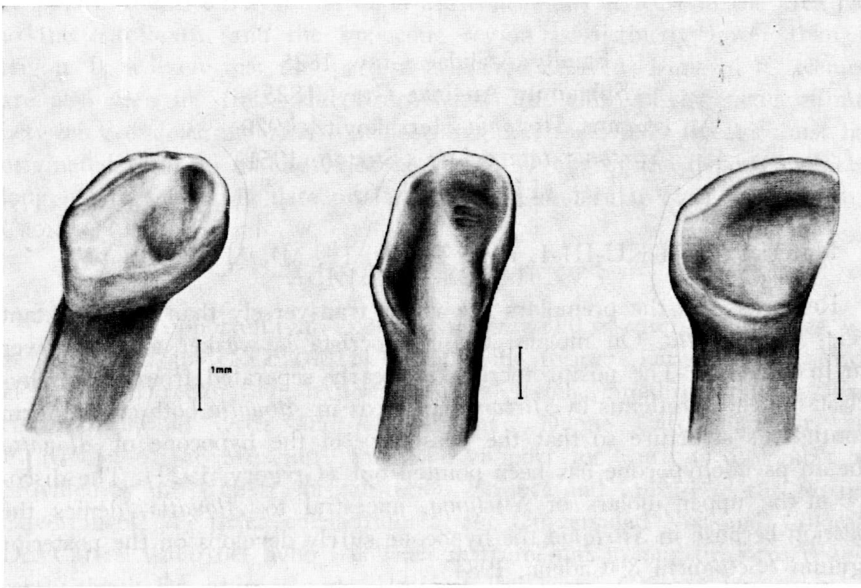

FIGURA 8. Incisors of marmosets, lingual view. IGM-KU-8402 (left), *Callithrix* (midle). and *Saguinus* (right). All are oriented with the I^1/I^1 interproximal facet vertical.

Callithrix/Cebuella/Leontopithecus clade. The molecular clock predicted the initial differentiation of the callitrichines at about 8-10 Ma and the origin of the *Callithrix/Cebuella* sublineage at 6-7 Ma (Sarich & Cronin, 1980). However, as the incisor provides evidence for the existence of species that are cladistically close to the *Callithrix/Cebuella* clade at 14 Ma, the previously branching lineage leading to *Saguinus,* and perhaps even that leading to *Leontopithecus,* must have differentiate earlier. Thus, as with platyrrhines generally, the new evidence points out a major discrepancy between the dates projected with the molecular clock and those based on paleontological evidence (Rosenberger, 1984; Setoguchi, 1985; Setoguchi & Rosenberger, 1985).

Genus indet.
(Fig. 3)

Material: IGM-KU-8403, left P_4

Remarks: It is smaller than *Neosaimiri* and close to *Callithrix jacchus* and related forms. The metaconid is a robust cusp separated widely from the protoconid, and the trigonid and talonid are about equal in length. The lingual slope of the metaconid is essentially vertical. This makes it unlikely that the tooth is a P_3, because in most extant callitrichines the P_3 metaconid is either poorly developed or, if present, has a strong lingual slope.

Family Atelidae Gray, 1825
Subfamily Atelinae Gray, 1825
Genus *Stirtonia* Hershkovitz, 1970
Stirtonia tatacoensis (Stirton, 1951)
(Figs. 4, 5 & 6)

Material: IGM-KU-III-1, right P^2, P^3, P^4, M^1, M^2

Remarks: All the premolars are wider transversely than in the extant species of *Alouatta.* On molars, the centrocrista is weaker and narrower than in *Alouatta.* The postprotocrista is clearly separated from the prehypocrista by the entoflexus in *Stirtonia,* whereas in *Alouatta* both cristae form a contiguous structure so that the possibility of the hypocone of *Alouatta* to be an pseudohypocone has been pointed out (Gregory, 1920). The discovery of the upper molars of *Stirtonia,* ancestral to *Alouatta,* denies the allocation because in *Stirtonia* the hypocone surely develops on the posterior cingulum (Setoguchi & Cadena, 1984).

The obvious difference in the dental morphology between *Stirtonia* and *Alouatta* is seen in the degree of robustness of the major cusps. In *Alouatta,* the major cusps and cristae herein are more robust than in *Stirtonia*. In *Stirtonia*, the major function of molars is grinding and partly crushing food material because no shearing blades are formed. On the contrary, in *Alouatta*, the major function in their occlusion is shearing food material (Setoguchi & Cadena, 1984). The differences in molar morphology result in a functional transformation from grinding or crushing food material in *Stirtonia* to shearing in *Alouatta*.

Genus *Kondous* Setoguchi, 1985
Kondous laventicus Setoguchi, 1985
(Fig. 9)

Material: IGM-KU-8201, right M^1 (type), IGM-KU-8202, right M^2
Diagnosis: Similar in size to *Stirtonia;* upper molar crowns rhomboidal and transverse, with large basin, low hypocone, reduced ectoloph, no lingual cingulum and single fused, platelike root.

Remarks: *Kondous* can be separated from *Stirtonia*, particularly, by the reduced ectoloph and stylar region, rhomboidal crown outline, fused roots and band-like instead of columnar lingual sidewall. The bluntness of M^1 cusps, modified root structure, and near continuity of trigon and talon, which are separated only buccally by a short crista obliqua, segregate *Kondous* from the ceboids. In *Kondous*, stylar elements are reduced, buccal cusps are low, the trigon and talon are continuous at least in the area close to the entoflexus, and the hypocone region is distinctly lower than the trigon. It is likely that this pattern is shared derived; some of its elements are also seen in *Ateles* and *Brachyteles*. The close phylogenetic affinities between *Kondous* and *Ateles* demostrates that the *Ateles* lineage must have originated prior to middle Miocene (14 Ma) age of the deposits which is long before the 5 Ma date predicted by the molecular clock of SARICH & CRONIN (1976).

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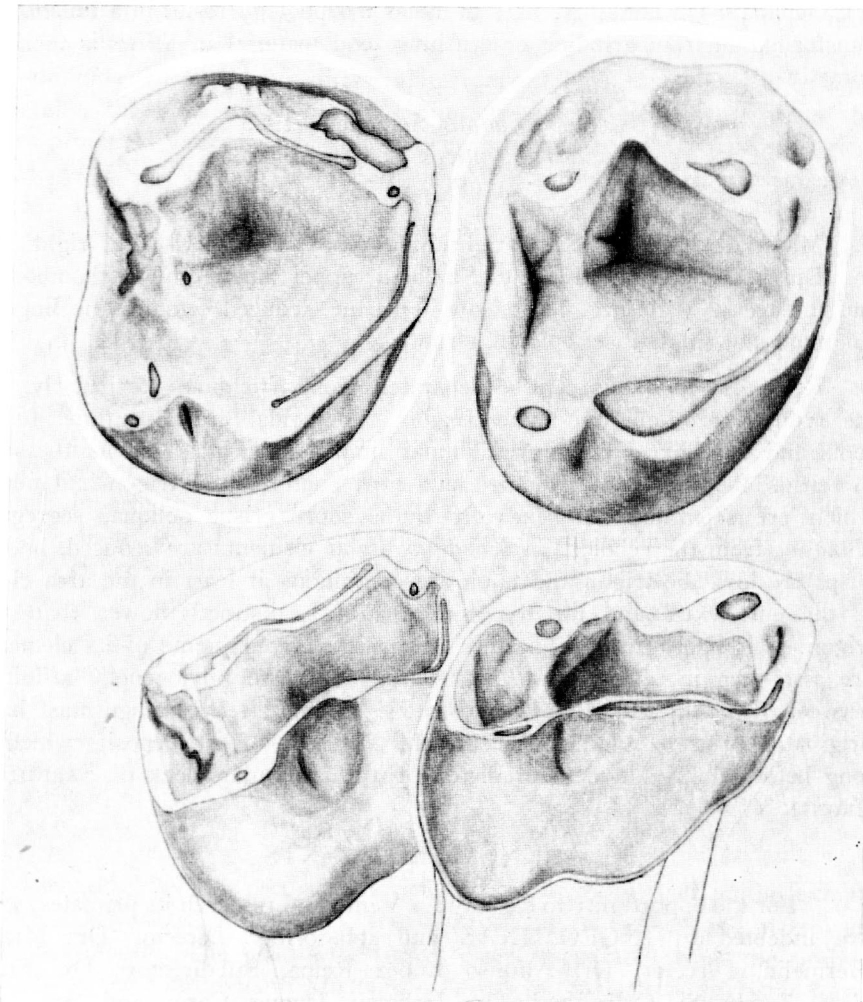

FIGURA 9. *Kondous laventicus.* Top right: IGM-KU-8201 (type), right M^1; top left: IGM-KU-8202, right M^2. Top pair by occlusal view, and, bottom pair by lingual view of the corresponding top pair, respectively.

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TABLE 1

Dimensions of fossil teeth (millimeters)

	Length	*Breadth*	*Height*
Micodon kiotensis, M^1, IGM-KU-8401:	2.5	3.2	—
Genus indet., I^2, IGM-KU-8402:	2.1	1.4	2.2
Genus indet., P$_4$, IGM-KU-8403:	2.1	2.1	—
Stirtonia tatacoensis, P^2, IGM-KU-III-1:	4.1	6.0	—
Stirtonia tatacoensis, P^3, IGM-KU-III-1:	4.5	6.8	—
Stirtonia tatacoensis, P^4, IGM-KU-III-1:	4.5	7.2	—
Stirtonia tatacoensis, M^1, IGM-KU-III-1:	6.3	7.2	—
Stirtonia tatacoensis, M^2, IGM-KU-III-1:	6.6	8.4	—
Kondous laventicus, M^1, IGM-KU-8201:	5.5	7.1	—
Kondous laventicus, M^2, IGM-KU-8202:	5.3	6.4	—